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## Condition mediates context-dependent breeding strategies and consequences

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# *Chapter 2*

Quality of breeders, but not timing of breeding, contributes to a seasonal decline in reproductive success of the hair-crested drongo: a novel comparative method

Lei Lv, Jan Komdeur, Jianqiang Li, Zhengwang Zhang

## Abstract

Seasonal declining reproductive success in many avian populations may be attributed to the deteriorating environment conditions over time (the “date hypothesis”), or to high quality individuals occupying superior territories and breeding earlier (the “quality hypothesis”). Different experimental approaches of manipulating the timing of breeding within a breeding season have been used to test these two hypotheses. However, as there is no direct control over the timing of breeding, manipulating the time of breeding indirectly may introduce potential confounding effects and misleading results. We tested the influence of timing of breeding on reproductive success in a socially monogamous passerine, the hair-crested drongo (*Dicrurus hottentottus*), by using a novel method of comparing the number of fledglings produced by the same perennial pair in the year of their earlier breeding with what they produced in the year of later breeding. In this species, birds produced fewer fledglings over the breeding season and this trend is consistent among years. Our results show that early breeders, who are in good quality and always laid earlier in the different years relative to the population mean, produced more fledglings than late breeders. Although there was no difference in clutch sizes between early breeders and late breeders, early breeders tended to have a higher survival rate of egg to fledgling. However, females of perennial pairs produced similar number of fledglings when they bred later compared to what they produced in other years. This pattern was true for both early and late breeders, who consistently started breeding earlier or later than the population mean, respectively. Our results supported the “quality hypothesis”, but not the “date hypothesis”. The seasonal decline in reproductive success in the hair-crested drongo, at least in perennial pairs, was due to the difference of quality between early breeders and late breeders. Our novel comparative method may offer a new powerful approach of testing the influence of actual timing of breeding on reproductive success.

## Introduction

For organisms living in seasonal environments, reproductive success is often affected by the timing of reproduction. In birds, the seasonal pattern in reproductive success has been documented in many species with most studies showing a consistent seasonal decline (Perrins 1970; Daan et al. 1988; Price et al. 1988). This seasonal pattern is especially true among bird species that generally fledge only one brood annually (Verhulst and Nilsson 2008). Such seasonal pattern may be attributed to the seasonal deteriorating environmental conditions over time, for example food availability (Hedgren and Linnman 1979; Verboven, Tinbergen, Verhulst, et al. 2001; Grübler and Naef-Daenzer 2008) and/or predation pressure (H G Smith 1993; Naef-Daenzer et al. 2001; Gotmark 2002). However, it may also result from high quality individuals occupying superior territories and breeding earlier than low quality breeders. As the effects of the actual timing of breeding are usually confounded with individual quality, it is often difficult to assess to what extent a seasonal decline in reproductive success is attributable to the effects of timing per se (the “date hypothesis”), as opposed to difference in quality between individuals (the “quality hypothesis”; Parsons 1975; Hatchwell 1991; Brinkhof et al. 1993; Christians et al. 2001). Disentangling the effects of actual timing of breeding and individual quality on seasonal decline in reproductive success is becoming increasingly important because of their potentially different influence on (avian) populations under global climate change (Both and Visser 2001; Miller-Rushing et al. 2010).

Experimental approaches of manipulating the timing of breeding within a breeding season have been used intensively to investigate whether the seasonal decline in reproductive success is due to the effect of timing independently of individual quality. Most of these manipulations have been carried out by either cross-fostering clutches that differed in laying dates (reviewed in Verhulst and Nilsson 2008), or by removing the first clutch that induces the breeding pair to produce a replacement clutch (reviewed in Nilsson 1999; Verhulst and Nilsson 2008). However, these manipulations can also alter the overall parental investment in the incubation period (cross-fostering) or the condition of females because of producing the first clutch which was removed. These side effects potentially have the same effect on subsequent reproductive success as the effect of the timing and, therefore, can have misleading results. For example, removing the first clutch can decrease a female’s condition due to producing an extra-clutch and consequently may negatively affect the survival of her chicks in the successive breeding attempt

(Smith et al. 1987; Nilsson and Svensson 1996). Hence, the decline in reproductive success of re-laying females can also be due to their decreased condition caused by the previous extra reproductive effort, and not to late breeding (Hansson et al. 2000). Overall, it is seemingly impossible to manipulate the timing of breeding without introducing the potential effects on other traits, because there is no direct control over the timing of breeding and we can only manipulate the time of breeding indirectly (Verhulst and Nilsson 2008).

A seasonal decline in reproductive success can be measured in each breeding season as the selection pressure on timing of breeding by regressing reproductive success against the timing of breeding. Although the selection pressure can change among years, the negative correlation between timing of breeding and reproductive success can be quite consistent in consecutive years (Charmantier et al. 2008; Reed et al. 2009). As the laying date of many iteroparous bird species is a heritable trait showing consistency within individuals (Noordwijk et al. 1981; Sydeman and Eddy 1995; Sheldon et al. 2003; Lourenço et al. 2011; Charmantier and Gienapp 2014), some females, who always lay earlier relative to the population mean (early breeders), may obtain a consistent higher reproductive success than later breeding females (late breeders) in such context. Meanwhile, there are also considerable variations in the laying dates within individuals in that females may lay earlier or later compared with their previous laying date. According to the “date hypothesis”, females have a lower reproductive success in the year of later breeding compared to the year of earlier breeding if other ecological factors (e.g. year effect) were controlled for or their influence was negligible. In contrast, the “quality hypothesis” predicts that reproductive success is not changed because the parental quality of individuals remain quite stable among years. We provide the first empirical test of this idea in a migratory passerine, the hair-crested drongo *Dicrurus hottentottus*. This species forms long-term socially monogamous pair bonds which offer a good opportunity to test this idea.

We tested whether actual timing of breeding influenced the reproductive success of perennial pairs, which keep pair-bonding in consecutive years, in hair-crested drongos. Perennial pairs of the hair-crested drongo are excellent candidates for testing this idea for the following reasons. First, the number of fledglings produced by perennial pairs declines with timing of breeding consecutively among years (see result). Second, the laying date of females in perennial pairs is repeatable among years (see method). Third, laying date and the number of fledglings produced by perennial pairs were not influenced by the duration of pair-bonding (years together) (Lv et al. 2016), which means that the

quality of perennial pairs was quite stable among years. Fourth, perennial pairs of the hair-crested drongos are highly faithful to their territory across years, therefore laying date or the number of fledglings produced by perennial pairs are less likely to be affected by the differences in territory quality among years because of switching territories and/or changes in territory quality. By comparing the number of fledglings produced by the same perennial pair in the year of their earlier breeding with what they did in the year of later breeding, we tested whether their decreased reproductive success was due to the difference in the quality of parents or the influence of actual breeding timing.

## Methods

### Study Species and Field Methods

Hair-crested drongos are medium-sized insectivorous songbirds in which males are slightly larger and brighter than females (Chen and Luo 1998). The species is distributed in the eastern South Asia, southern and eastern East Asia and Southeast Asia, and the population that breeds in central and southern of China (including our study site) is traditionally thought to overwinter in Indochina (Rocamora and Yeatman-Berthelot 2009). The data used in this study were collected each year between 2010 and 2015 in the study area (ca 400 ha) consisting of broadleaf forest, situated in the Dabieshan Mountains, Dongzhai National Nature Reserve (31.95 °N, 114.25 °E, elevation 100-840 m). Birds arrive in late April at our study site, and leave before the middle of October (Z Gao et al. 2006). Breeding starts about one week after arriving. Both parents participate almost equally in all breeding activities, including nest building, incubation and feeding of offspring (Chen and Luo 1998). Modal clutch size is four (75.64%, range 3-5,  $N = 275$ ), and both median incubation period and nestling period are 17 days. The hatching rate is high (92.8%,  $N = 484$ , L. Lv, unpublished data) and, due to an abundance of food, no nestlings died of starvation if they were not predated (208 nests monitored from hatching to fledgling, L. Lv, unpublished data). As both parents defend their nests aggressively against predators during the breeding season, it resulted in about two thirds of all nests producing at least one fledgling. The main reason for unsuccessful breeding is nest predation by predators such as Eurasian Jays (*Garrulus glandarius*) and Besra Sparrow Hawks (*Accipiter virgatus*) (L. Lv personal observation).

Each year, we located nests by checking trees which had been used previously or searching the forest for nests systematically. Whether parental birds were ringed

as well as their identity (according to combination of colour rings) was determined either through direct observation with a telescope or binoculars or indirectly through video recordings. The latter were taken by placing video cameras (Sony HDR-160E, Sony HDR-260E or Samsung F40) at approximately 20 metres from the nest. Un-ringed parents were captured by mist-netting in close proximity to their nest trees during incubation or the nestling period. Birds were marked individually with a metal ring and a unique combination of three colour rings. Sex of the adults was determined by brood patch size because these were distinctively larger for females than males. Nests were checked every one to three days by mirroring over nests or climbing trees to determine laying date, clutch size, hatching date, number of nestlings and number of fledglings.

### **Data Analyses**

To quantify the strength of selection on laying date in each year, we regressed number of fledglings against laying date by using linear models for all females (including females of perennial pairs), and for females of perennial pairs, respectively. Although the number of fledglings was always negatively correlated with laying date, the selection on laying date was significant only in some years (Table 2.1). Therefore, a linear mixed model with the number of fledglings produced by perennial pairs as the response variable was used to test the effect of laying date on the number of fledglings within the whole study period. The full model included ‘laying date’, ‘pair-bond duration’ and ‘year of pair-bond duration’ as fixed effects, and ‘year’ and ‘pair ID’ as random effects. The final model demonstrated that the number of fledglings produced by perennial pairs declined with the timing of breeding (Table 2.2). As the laying date of females in perennial pairs is repeatable ( $r = 0.525 \pm 0.074$ , range: 0.365 – 0.655,  $N = 71$ ,  $p < 0.001$ ), we investigated whether perennial pairs produced fewer fledglings when they laid later compared to what they produced in other years by using within-subject centring (van De Pol and Wright 2009). ‘Laying date’ in the former model was replaced by ‘mean laying date’ within perennial pairs, ‘difference from mean laying date’ of each perennial pair in each year, and their two-way interaction. If the number of fledglings was affected, we applied the same model with clutch size as the response variable to test whether the reduction in production of fledglings by perennial pairs was a consequence of lower clutch size. After that, a generalized linear mixed model, with Poisson distribution and log link, was carried out to test whether the survival rate of egg to fledgling was also affected or not.

Laying date of each nest was standardized by subtracting the mean laying date

of the population in any given year. Statistical analyses were performed in R.3.1.1 (R Core Team 2014) with the package lme4 (Bates et al. 2014) for mixed-effect modelling and the package “rptR” (Schielzeth and Nakagawa 2011) for calculating repeatability. Repeatability values and confidence intervals were calculated based on a restricted maximum likelihood method (REML). Estimates and *p* values (based on permutations) were calculated using 1000 bootstrapping and permutation runs. We used an Information-Theoretic (IT) model selection approach, based on the Akaike information criterion (Burnham and Anderson 2002) with the Hurvich and Tsay correction for finite sample size (AICc). Model parameters were dropped if doing so resulted in a lower AICc score, which were obtained by using the “AICcmodavg” package (Mazerolle 2011), but ‘laying date’ or ‘mean laying date’ and ‘difference from mean laying date’ were always kept in the final models.

## **Results**

### **Selection on Laying Date**

The earliest breeding pairs of the hair-crested drongo start laying in mid-May and the mean laying date of the population is late May or early June (Table 2.1). The latest breeding pairs lay in mid-June (Table 2.1), which can be 30 days later than the date of the first egg in the population in that year. The laying date of the same female of a perennial pair in different years differed from 0 to 18 days.

The results of the linear models examining selection on laying date each year for all females and females of perennial pairs are summarized in Table 2.1. Significant negative correlation between timing of breeding and reproductive success was detected in 3 out of 6 years for all females, and 1 out of 6 years for females of perennial pairs (Table 2.1). The negative correlations between laying date and number of fledglings was consistent both for all females present in the populations as well as for females of perennial pairs in all the years (Table 2.1). Furthermore, for the entire study period, the number of fledglings produced by the females of perennial pairs declined significantly with delayed onset of breeding (Table 2.2).



**Table 2.1** Temporal patterns of selection on relative laying date of the hair-crested drongo. LD<sub>first</sub> = date of the first egg laid in the population. LD<sub>mean</sub> = mean laying date of the population. LD<sub>last</sub> = laying date of the last breeding pairs in the population.  $N$  = number of breeding pairs monitored each year. Linear terms ( $\beta$ ) indicate the strength of directional selection.  $P$  values are actual values from linear models. Subscript  $p$  = perennial pairs used in the later analyses. Only the first nest of breeding pairs in the breeding season was used. Relative laying date was used through standardising laying date by subtracting the mean laying date of the population in that specific year. Significant values are denoted in bold face.

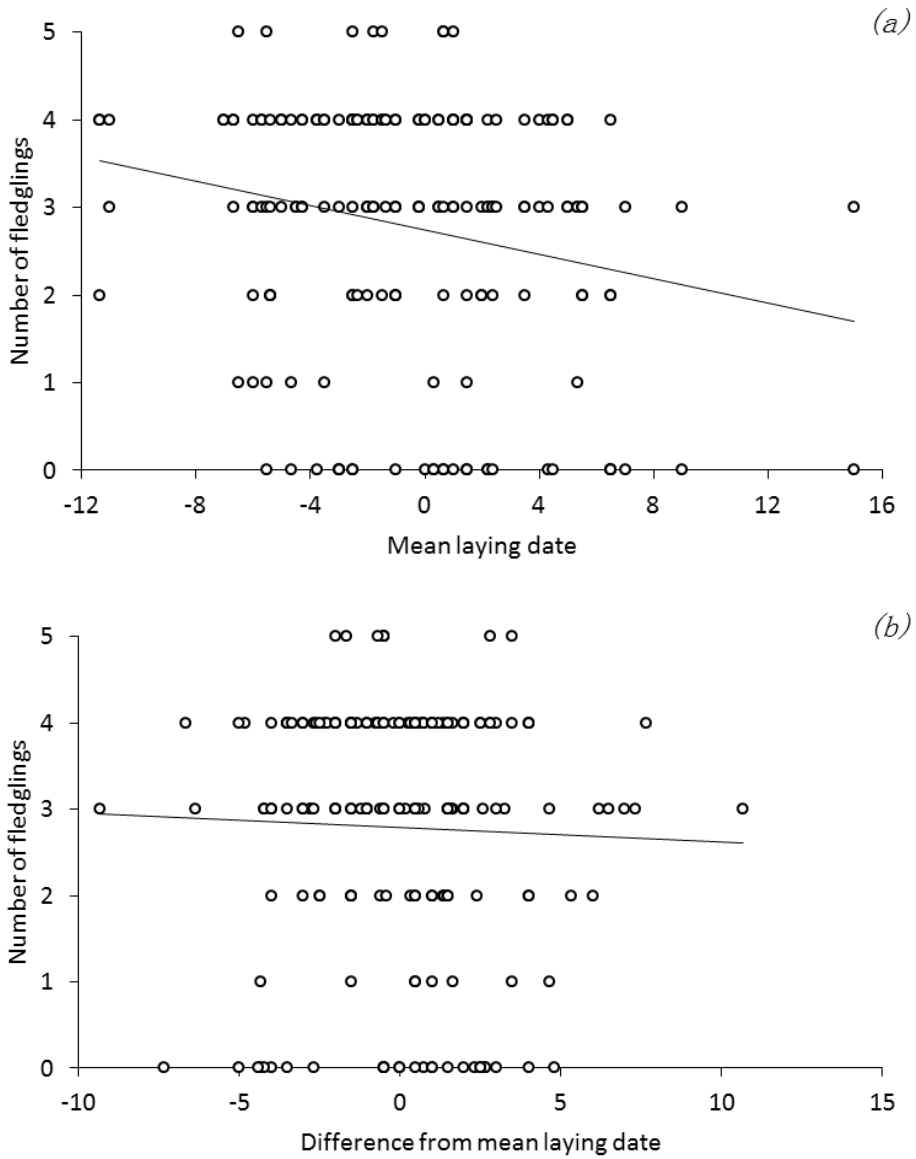
| Year | LD <sub>first</sub> | LD <sub>mean</sub> | LD <sub>last</sub> | $N$ | $\beta$ | SE    | $t$   | $P$          | $N_p$ | $\beta_p$ | SE <sub>p</sub> | $t_p$ | $P_p$        |
|------|---------------------|--------------------|--------------------|-----|---------|-------|-------|--------------|-------|-----------|-----------------|-------|--------------|
| 2010 | 14-May              | 27-May             | 9-June             | 42  | -0.051  | 0.037 | -1.37 | 0.177        | 15    | -0.036    | 0.052           | -0.69 | 0.503        |
| 2011 | 16-May              | 28-May             | 8-June             | 85  | -0.088  | 0.031 | -2.81 | <b>0.006</b> | 33    | -0.084    | 0.044           | -1.89 | 0.069        |
| 2012 | 11-May              | 21-May             | 14-June            | 77  | -0.027  | 0.032 | -0.83 | 0.409        | 35    | -0.039    | 0.052           | -0.75 | 0.456        |
| 2013 | 15-May              | 29-May             | 14-June            | 79  | -0.023  | 0.034 | -0.67 | 0.503        | 39    | -0.019    | 0.052           | -0.36 | 0.719        |
| 2014 | 19-May              | 1-Jun              | 18-June            | 85  | -0.073  | 0.028 | -2.62 | <b>0.010</b> | 37    | -0.016    | 0.048           | -0.34 | 0.737        |
| 2015 | 12-May              | 24-May             | 11-June            | 81  | -0.079  | 0.035 | -2.28 | <b>0.025</b> | 28    | -0.116    | 0.048           | -2.41 | <b>0.023</b> |

**Table 2.2** Summary of three linear mixed models investigating whether laying date, mean laying date of perennial pairs and the difference of laying date from mean laying date of perennial pairs in each year (2010-2015) influence the number of fledglings and clutch size in hair-crested drongos. 187 breeding attempts of 71 breeding pairs were used in the analysis. Significant effects are denoted in bold face.

| Fixed effects                    | Estimates | SE    | df     | <i>t</i> -value | <i>p</i> -value |
|----------------------------------|-----------|-------|--------|-----------------|-----------------|
| Number of fledglings:            |           |       |        |                 |                 |
| Laying date                      | -0.054    | 0.020 | 143.42 | -2.69           | <b>0.008</b>    |
| Number of fledglings:            |           |       |        |                 |                 |
| Mean laying date                 | -0.071    | 0.024 | 81.16  | -2.91           | <b>0.005</b>    |
| Difference from mean laying date | -0.018    | 0.036 | 120.07 | -0.52           | 0.607           |
| Clutch size:                     |           |       |        |                 |                 |
| Mean laying date                 | -0.010    | 0.011 | 69.30  | -0.92           | 0.362           |
| Difference from mean laying date | 0.008     | 0.014 | 86.38  | 0.60            | 0.551           |

**Table 2.3** Summary of a generalized linear mixed model investigating whether mean laying date of perennial pairs and the difference of laying date from mean laying date of perennial pairs in each year (2010-2015) influence the survival rate of egg to fledgling in hair-crested drongos. 187 breeding attempts of 71 breeding pairs were used in the analysis.

| Fixed effects                    | Estimates | SE    | <i>z</i> -value | <i>p</i> -value |
|----------------------------------|-----------|-------|-----------------|-----------------|
| Mean laying date                 | -0.025    | 0.013 | -1.85           | 0.064           |
| Difference from mean laying date | -0.009    | 0.020 | -0.45           | 0.651           |



**Figure 2.1** (a) The influence of mean laying date of perennial pairs of the hair-crested drongo, and (b) the difference of laying date from mean laying date of perennial pairs in each year (2010-2015) on the number of fledglings in hair-crested drongos. 187 breeding attempts of 71 breeding pairs. The corrected correlation coefficients based on linear mixed model was (a)  $r^2 = -0.071 \pm 0.024$  ( $p = 0.005$ ) and (b)  $r^2 = -0.018 \pm 0.036$  ( $p = 0.607$ ).

**Selection on Difference of Laying Date Among and Within Pairs**

Early breeding females of perennial pairs fledged more nestlings than later breeding females of perennial pairs (Table 2.2, Figure 2.1a). However, females did not produce fewer fledglings when they bred later compared to the number of fledglings that they produced in other years (Table 2.2, Figure 2.1b). This pattern is consistent in early breeders and late breeders (Table 2.2, the interaction of ‘mean laying date’ and ‘difference from mean laying date’ was dropped from the full model). Although there is no difference in clutch sizes between early breeders and late breeders (Table 2.2), the survival rate of egg to fledgling tended to be higher in early breeders (Table 2.3). Neither clutch size nor the number of fledglings per egg in the nest were affected when females of perennial pairs bred later compared to what they produced in other years (Table 2.2, Table 2.3) and there was no different trend between early breeders and late breeders.

**Discussion**

In the hair-crested drongo, reproductive success, in terms of number of fledglings produced per clutch, was negatively correlated with laying date and this seasonal pattern is consistent among years. By comparing the number of fledglings produced by the same pair when they bred later in a given year compared to what they did in the other years, we found that perennial pairs did not produce fewer fledglings when they bred relatively later. However, early breeders produced more fledglings than late breeders, because they tended to have a higher survival rate of egg to fledgling. Therefore, our results support the “quality hypothesis”, but not the “date hypothesis”, that the seasonal decline in reproductive success of the hair-crested drongo, at least in perennial pairs, was due to high quality breeders starting to breed earlier than low quality breeders.

**Timing of Breeding and Quality**

In perennial pairs of the hair-crested drongo, early breeding females produced more fledglings than late breeding females, because they tended to have a higher survival rate of egg to fledgling than late breeders. Timing of breeding has been usually related to individual quality in birds. In long-distance migratory bird species, high quality individuals who were in better condition (Ninni et al. 2004) and/or have lower parasite infestation (Møller et al. 2004) arrive early at the breeding area and, therefore, get priority of occupying or retaining high quality territories that are rich in food (Daan et al. 1990) and/or situated far from the nest of the avian predators.

Meanwhile, a positive correlation between arrival dates and laying dates has been documented in many migratory species (Potti 1998; Höcker 2002; Vergara et al. 2007, but see Lourenço et al. 2011). High quality individuals occupying high quality territories and breeding early are likely to obtain higher reproductive success independent of breeding timing (Nilsson and Svensson 1993). Therefore, a consistent seasonal decline in reproductive success in the hair-crested drongo could be attributable to a difference in quality of individuals and/or their occupied territories between early breeders and late breeders.

### **Timing of Breeding and Environmental Conditions**

Female hair-crested drongos of perennial pairs produced similar number of fledglings when they bred later in a given year compared to other years. As the laying date and the number of fledglings produced by perennial pairs of the hair-crested drongo were not affected by the pair-bonding duration (Lv et al. 2016), it suggested that the relative phenotypic quality of perennial pairs (with respect to the whole population) is more or less constant among years. Furthermore, perennial pairs of the hair-crested drongo are highly faithful to their territories (88.7% use the same territory in this study,  $N = 71$ , L. Lv unpublished data). Therefore, it indicated that the actual timing of breeding did not influence reproductive success of hair-crested drongos and breeding pairs, at least perennial pairs, did not produce fewer fledglings when they bred relatively later. In this species, the main reason of nest failure is predation by avian predators such as Eurasian Jays during the incubation period and Besra Sparrow Hawks during nestling period. For all failed nests, 30.2% failed during incubation period, and 69.8% failed during the nestling period ( $N = 139$ , L. Lv, unpublished data). Avian predators usually have fledglings near the peak fledging of their preys (Gotmark 2002), therefore breeding earlier has been reported to be advantageous in avoiding the time when avian predators have high food requirement to feed their nestlings (H G Smith 1993; Naef-Daenzer et al. 2001; Gotmark 2002). However, this may not be the case in hair-crested drongos. Besra Sparrow Hawks, a common avian predator in our study area, usually have fledglings in the middle of June (L. Lv, personal communication). Therefore, early breeders of the hair-crested drongo, who usually have fledglings in the end of June, may face a similar predation pressure as their late breeding conspecifics. In terms of predation pressure, environmental conditions may not deteriorate over breeding season.

### **Interaction between Quality and Environmental Conditions**

High quality individuals may obtain similar reproductive success even when they breed later in a given year compared to other years, because they may be able to compensate for the negative effects of late breeding (De Neve et al. 2004; Verhulst and Nilsson 2008). If this is the case, the reproductive success of early breeders, who are good quality individuals, may not decrease even when they bred relatively later, but not for the late breeders who are low quality individuals. However, this is not the case in hair-crested drongos since there is no significant interaction between ‘mean laying date’ and ‘difference from mean laying date’. Both early and late breeders produced similar numbers of fledglings when they bred later compared to what they did in other years. It highlights that environmental conditions did not deteriorate over the breeding season.

### **Conclusion**

By using a novel method of comparing the reproductive success of the same pair of hair-crested drongos among years when their timing of breeding was different relative to the population mean, we demonstrated that the observed seasonal decline in reproductive success, at least in perennial pairs, was due to high quality individuals breeding earlier than low quality conspecifics, but not to the effect of time of breeding per se. This new method of analysis offers a powerful alternative to experimental approaches to investigate whether a seasonal decline in reproductive success is affected by actual timing of breeding.

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An adult drongo lands on the trunk of its nest tree to peel off barks.

*Photo: Peng Zhang*